

Creek habitats as sources for the spread of an invasive herb in a New Zealand mountain landscape

Alice L. Miller^{1,2*}, Susan K. Wiser³, Jon J. Sullivan^{1,4} and Richard P. Duncan^{1,5}

¹BioProtection Research Centre, PO Box 84, Lincoln University, Lincoln 7647, New Zealand

²Current address: Pyramid Botanical Consultants, 3001 Carriage Drive, Estes Park, CO 80517, USA

³Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

⁴Department of Ecology, PO Box 84, Lincoln University, Lincoln 7647, New Zealand

⁵Institute for Applied Ecology, University of Canberra, ACT 2601, Australia

*Author for correspondence (Email: milleralicelee@gmail.com)

Published online: 28 July 2014

Abstract: Landscapes typically comprise various habitats that differ in their susceptibility to invasion by exotic species. Highly invulnerable habitats such as riparian corridors can act as a conduit for rapid movement across the landscape and as a propagule source to facilitate spread into adjacent, less invulnerable habitats. If this is so, there should be a decline in invader frequency and/or abundance with distance away from the source; the local abundance of invasive species in the source habitat should be positively correlated with local abundance in the adjacent habitat; and, having accounted for variation in local source population size, the slope of the decline in invader abundance with distance away from the source habitat should reflect the ease with which adjacent habitat can be invaded. Here, we test these predictions to assess whether creek habitats function as a source to facilitate the spread of the invasive plant *Hieracium lepidulum* Stenstr. (Asteraceae) in upland catchments of the South Island, New Zealand, by surveying *H. lepidulum* abundance in creek margin and adjacent beech forest and subalpine habitat in 17 creek catchments. Our results imply that propagule pressure from populations in creek margins and other disturbed areas is driving catchment-wide *H. lepidulum* invasion, but forest and subalpine habitats currently differ in the way *H. lepidulum* spreads from source populations. Our results suggest that *H. lepidulum* invasion is at an earlier stage in subalpine areas, that there are few barriers to invasion across this habitat, and that subalpine habitats will become more heavily invaded than forests. These findings can be used to underpin monitoring strategies and management prioritisation for this invader.

Keywords: *Hieracium lepidulum*; habitat invulnerability; invasion; propagule pressure; riparian habitat; spread dynamics

Introduction

Landscapes typically comprise a mixture of habitats that can differ in the degree to which they are susceptible to invasion by exotic species (Elton 1958; Rejmánek 1989; Richardson et al. 2000; Chytrý et al. 2008b). Such variation is often key to understanding the spread of invasive species because highly invulnerable habitats can act as a conduit for rapid movement across the landscape, and as a propagule source to facilitate spread into adjacent, less invulnerable habitats (e.g. Forcella & Harvey 1983; Gelbard & Belnap 2003; Sullivan et al. 2009). The role of highly invulnerable habitats as sources facilitating spread into adjacent habitats will depend on at least three factors: (1) the rate at which invasive populations build up in source areas and hence the rate at which they can supply propagules for further spread (e.g. Dias 1996; Meekins & McCarthy 2002; Harris et al. 2011); (2) the degree to which adjacent habitats differ from source areas in terms of invulnerability, whereby habitats highly resistant to invasion will require a greater input of propagules to overcome that resistance (e.g. D'Antonio et al. 2001; Von Holle & Simberloff 2005; Chytrý et al. 2008a); and (3) propagule movement, with dispersal barriers, such as those created by forest edges, potentially limiting propagule movement from source into adjacent habitats (Cadenasso & Pickett 2001; With 2002).

Linear habitat networks, such as riparian and road corridors, are known for their susceptibility to invasion because they are often highly disturbed, have relatively high resource availability, and are subjected to high levels of propagule pressure (e.g. DeFerrari & Naiman 1994; Stohlgren et al. 1999; Sullivan et al. 2009). Many studies have inferred from the relative abundance of invasive species in riparian and road corridors that these areas function as source habitats for the spread of invasive species into adjacent less invulnerable habitats (e.g. Brothers & Spingarn 1992; Naiman & Décamps 1997; Watkins et al. 2003). For example, if highly invaded habitats such as riparian corridors act as a source for invasive species spread into adjacent habitat then we would expect a decline in invader frequency or abundance with distance away from the source (Harrison et al. 2002; Gelbard & Belnap 2003; Hansen & Clevenger 2005; Flory & Clay 2006). While this pattern has been well documented, two additional predictions associated with the source habitat hypothesis may provide further insight into the spread of invaders: (1) if the rate of spread into adjacent habitat is limited by propagule availability, due to dispersal limitation or because large numbers of propagules are required to overcome invasion resistance, then the local abundance of invasive species in the source habitat should be positively correlated with local abundance in the adjacent habitat. In other words, local spread into adjacent habitat should be facilitated by greater propagule pressure associated with larger

local source populations; (2) having accounted for variation in local source population size, the slope of the decline in invader abundance with distance away from the source habitat should reflect the ease with which adjacent habitat can be invaded. Habitats that are difficult to invade, due to dispersal barriers, such as that provided by forest edges (Cadenasso & Pickett 2001; With 2002) or because large numbers of propagules are required to overcome resistance to invasion, should have steep slopes with invader abundance dropping rapidly with distance from the source, while more readily invaded habitats should have shallower slopes. Here we test these predictions with the aim of determining whether creek corridors function as a source habitat to facilitate the spread of the invasive herb *Hieracium lepidulum* Stenstr. (Asteraceae) (Fig. 1) in montane and subalpine catchments of the South Island, New Zealand.

Hieracium lepidulum is an invasive herb that has increased dramatically in abundance throughout the South Island in recent decades and is now present in a wide range of upland habitats from modified short-tussock grassland to intact beech forest to high alpine herb fields (Rose et al. 1995; Duncan et al. 1997; Rose et al. 1998; Wiser et al. 1998; Wiser & Allen 2000; Miller 2006). Historical data indicate that *H. lepidulum* is over-represented in naturally disturbed habitats such as creek margins and forest canopy gaps (Wiser & Allen 2000; Spence et al. 2011). We test three hypotheses to determine whether creek margin habitats are acting as a source for spread: first, density of *H. lepidulum* should decline with distance away from creeks; second, local density of *H. lepidulum* in adjacent habitat should be positively correlated with local density in creek habitat; and third, the strength of this correlation should decline with

distance from the creek. Because forest is likely to provide a less permeable barrier for seed dispersal for this short-statured, wind-dispersed herb relative to shrub and tussock grassland vegetation in subalpine areas, we analysed data from forest and subalpine habitats separately. Our expectation is that the decline in *H. lepidulum* density with distance from the creek should be less pronounced in subalpine than in forest habitat. We attempt to control for the effects of environmental variation that might also explain differences in *H. lepidulum* abundance by including overhead canopy cover, distance from the creek mouth, elevation, and local disturbance as covariates in our analysis. We make the assumption that higher local abundance in creek margin habitats is associated with higher propagule pressure from these habitats, i.e. that total seed output is positively correlated with population size.

Materials and methods

Study area

Our study was carried out in creek catchments in Craigieburn Forest Park on the eastern side of the Southern Alps, Canterbury, New Zealand (Fig. 2). This area was chosen because it has the longest known history of *H. lepidulum* invasion in New Zealand (Rose et al. 1995; Wiser et al. 1998) meaning that *H. lepidulum* was sufficiently common that we could accurately quantify its spatial distribution. The landscape of the park is mountainous with elevations ranging from 800 to 2000 m above sea level. Mean annual temperature is 8.0°C and mean annual precipitation is 1447 mm (McCracken 1980). Soils are Allophanic Brown Soils derived from greywacke, loess and colluvium (Hewitt 2010). Old-growth mountain beech forest (*Fuscospora cliffortioides*) is the dominant vegetation type from approximately 800 to 1400 m elevation, giving way to subalpine scrub, tussock grasslands dominated by *Chionochloa* spp., and alpine herbfields at higher elevations.

Data collection

During January to May 2003, we quantified the abundance of *H. lepidulum* in creek margin habitat (defined as the area between frequently flooded, sparsely vegetated creek gravels and the edge of the adjacent closed forest or subalpine habitat) and at increasing distances into adjacent forest and subalpine habitats in 17 creeks (Fig. 2). To select creeks for study, we



Figure 1. *Hieracium lepidulum* growing in a creek corridor in Craigieburn Forest Park.

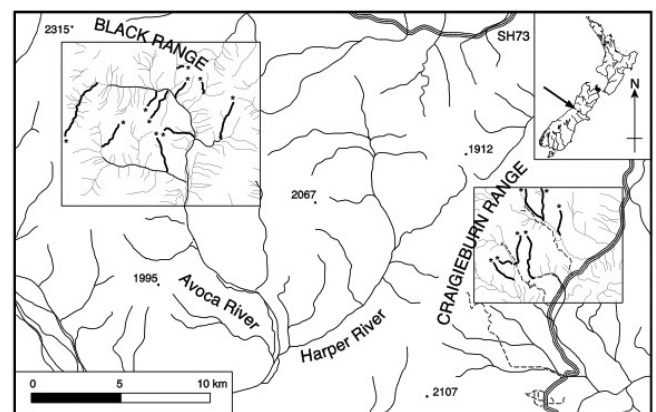


Figure 2. Location of study area with the 17 surveyed creeks in bold and indicated by an asterisk.

first divided the area into the two main catchments: the Avoca River and Craigieburn Stream. The Avoca River catchment was then divided into 10 strata defined by distance up the main Avoca River Valley, excluding lower elevation areas that had been extensively modified by burning and livestock grazing. Within each stratum one creek was randomly chosen for survey from NZ260 topographical maps with the constraint that creeks were required to be longer than 1 km and to extend into subalpine habitat. In the Craigieburn Stream catchment all seven creeks that were longer than 1 km and not modified by ski-field development or roading were surveyed.

For each creek, transects running perpendicular from the creek margin and extending 100 m into the adjacent habitat were placed at 100-m intervals up the creek, beginning at a random point 0–50 m from the creek mouth, until either creek margin habitat was no longer distinguishable from the surrounding subalpine habitat, or the terrain became inaccessible. Which side of the creek to sample was randomly determined at each sampling point. Each transect comprised five plots, each 2×3 m, located at: (1) a random point within the creek margin (creek); (2) in the forest or subalpine habitat immediately adjacent to the creek margin (edge); (3) at 10 m; (4) at 30 m; and (5) at 100 m away from the creek margin into the adjacent habitat.

Each plot was subdivided into six 1×1 m quadrats, and the number of *H. lepidulum* plants within each quadrat was counted and the total number of plants summed and converted to a density (plants/m²). At each plot, we recorded the elevation (metres above sea level) and whether the plot showed evidence of past disturbance (excluding flood disturbance in creek margin habitat), defined as a treefall gap, uproot mound, landslide or frost heave. For plots in forest habitat, we visually assessed the percentage of overhead canopy cover using the scale: 0 = 0%, 1 = >0–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%.

Data analysis

We measured 1144 plots on 229 transects in the 17 creeks, with the number of transects per creek ranging from 25 to 109. We used the 915 plots in habitat adjacent to creek margins for analysis, treating the density of *H. lepidulum* in creek-margin plots at the start of each transect as a covariate (see below). Of the 915 plots in non-creek-margin habitat, 636 (70%) had no *H. lepidulum* plants, with densities in the remainder ranging from 0.2 to 482.0 plants/m². Because these data were strongly zero-inflated, we used a two-step approach, first modelling the probability that *H. lepidulum* was present in a plot or not as a function of covariates, and second, where *H. lepidulum* was present, modelling the log-transformed density as a function of covariates (Fletcher et al. 2005). This two-step approach allowed us to distinguish factors associated with both establishment (presence or absence) and local abundance given establishment, with mean density being the product of these.

To test the first hypothesis, that density of *H. lepidulum* declines with distance away from the creek margin, we fitted models that included only distance of the plot from the creek (with edge plots assigned a distance of 1 m) as an explanatory variable. Transect and creek identity were included as nested random effects to accommodate the nesting of plots within transects and transects within creeks. To test the second hypothesis, that local density of *H. lepidulum* in adjacent habitat should be correlated with local density in creek margin habitat, and to assess whether any decline in *H. lepidulum* density with distance away from the creek could be attributed to changes in other covariates, we fitted models with plot distance from creek, density of *H. lepidulum* in the creek

margin, elevation, disturbance, distance of transect from creek mouth (this was tested in addition to elevation to examine whether *H. lepidulum* spread up catchments from lower-valley propagule sources, while elevation is related to environmental suitability for invasion), and canopy cover (for plots in forest habitat only) as explanatory variables. Again random effects were included to account for the nested survey structure. Disturbance was a binary variable (disturbed or not), coded as 1 or 0. Canopy cover was treated as a continuous variable, with all remaining continuous variables (distance away from creek, density of *H. lepidulum* in the creek margin, elevation and distance of transect from creek mouth) log-transformed to put them on a multiplicative scale. All continuous variables were then standardised by subtracting the mean and dividing by two standard deviations, to put the regression coefficients, including those for the binary variables, on a comparable scale (Gelman & Hill 2006).

We modelled *H. lepidulum* presence/absence on plots by specifying a binomial distribution and logit link, and modelled log-transformed density given presence by specifying a normal distribution and identity link. To test our third hypothesis, that the strength of the relationship between density in a plot and density in the adjacent creek margin should decline with distance from the creek, we estimated a separate parameter for this relationship for each distance class (edge, 10 m, 30 m and 100 m away from the creek) by running a separate model for each distance class.

In all analyses, the random-effect terms for creek identity were assumed to be drawn from a normal distribution with mean zero and variance estimated from the data, while the random-effect terms for transect identity were assumed to be drawn from a normal distribution with mean given by the creek identity and variance estimated from the data. We fitted the models in a Bayesian framework to readily accommodate the hierarchical structure of the data. We specified non-informative prior distributions for the parameters to allow data to drive estimation. All regression coefficients were assigned normal prior distributions with mean 0 and variance 1000, while variance terms were given broad uniform priors (0–100) on the standard deviation following Gelman (2006). Models were fitted using OpenBugs v2.10 (Thomas et al. 2006) called using the BRugs package from R 2.8.1 (R Development Core Team 2008) and run with three chains for 10 000 iterations, with a burn-in of 10 000 iterations, which was sufficient to achieve convergence (judged by visually inspecting the chain histories).

Results

In support of our first hypothesis, in both forest and subalpine habitats the probability of occurrence of *H. lepidulum* declined with increasing distance from the creek margin (Fig. 3a, b). In forests the abundance of *H. lepidulum* when it was present also declined with increasing distance from the creek, whereas in subalpine habitat there was no clear relationship between *H. lepidulum* abundance when present and distance (Fig. 3c, d). The slope of the relationship between the probability of *H. lepidulum* occurrence and distance from the creek margin was more negative in forest relative to subalpine habitat, suggesting a steeper drop-off in occurrence with distance in forest (Fig. 4a). When we included in the model other covariates that might explain variation in the presence or abundance of *H. lepidulum* (density of *H. lepidulum* in the creek margin, elevation, disturbance, distance of transect from creek mouth,

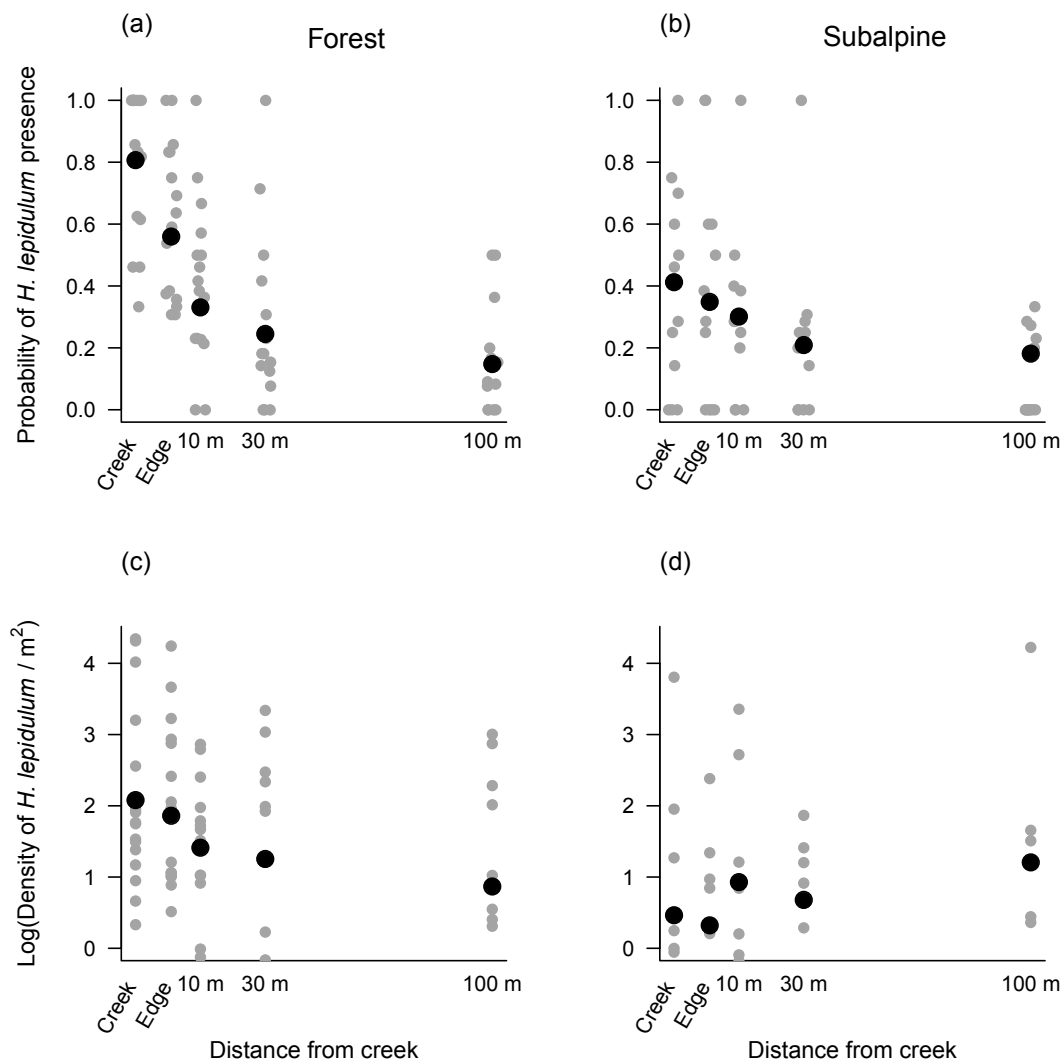


Figure 3. (a, b) Probability of *Hieracium lepidulum* presence (the proportion of plots containing at least one *H. lepidulum* plant) for forest and subalpine plots in each of 17 creeks (grey circles) in Craigieburn Forest Park as a function of distance from the creek. Black circles show the overall mean probability for each distance. (c, d) Mean log density of *H. lepidulum* where it was present for forest and subalpine plots (grey circles) as a function of distance from creek. Black circles show overall mean densities for each distance. Creek = creek margin habitat, Edge = forest or subalpine habitat immediately adjacent to the creek margin.

and canopy cover), only the probability of *H. lepidulum* occurrence in forest habitats remained significantly correlated with distance from the creek (Fig. 4b).

The probability of *H. lepidulum* occurrence in forest and subalpine habitat was positively related to local abundance in creek margin habitat, and the strength of that relationship declined with increasing distance away from the creek (Fig. 5a), in support of our second and third hypotheses. The local abundance of *H. lepidulum*, where present in forests, was also positively related to abundance in local creek margin habitat, but there was no obvious decline in the strength of this relationship with distance from the creek (Fig. 5b). In subalpine habitats, *H. lepidulum* abundance where present was not clearly related to local abundance in creek margins at any distance (Fig. 5b).

Hieracium lepidulum was more likely to occur in disturbed plots in both forest and subalpine habitats, and in forest plots with lower overhead canopy cover (Fig. 5c). It was more likely to occur in forest plots at higher elevation and in subalpine plots at lower elevation (Fig. 5c). Distance from creek mouth had

no clear effect on the probability of *H. lepidulum* occurrence (Fig. 4c). Local abundance of *H. lepidulum*, where present in the forest, was higher where overhead canopy was lower. Other covariates were not strongly related to abundance (Fig. 5d).

Discussion

Our results strongly support the idea that creek margin habitats function as a source for the spread of *H. lepidulum* into adjacent forest and subalpine habitats in New Zealand's eastern mountain landscape. A key determinant of the extent of spread into adjacent habitats is the size of local creek margin populations, with larger source populations in creek margins associated with a higher probability of occurrence in adjacent habitats. This suggests that establishment into adjacent habitat is driven by propagule pressure from local source populations, although subsequent invader abundance, at least in the forest, appears to be determined more by local environment and disturbance history than by dispersal from creek habitat.

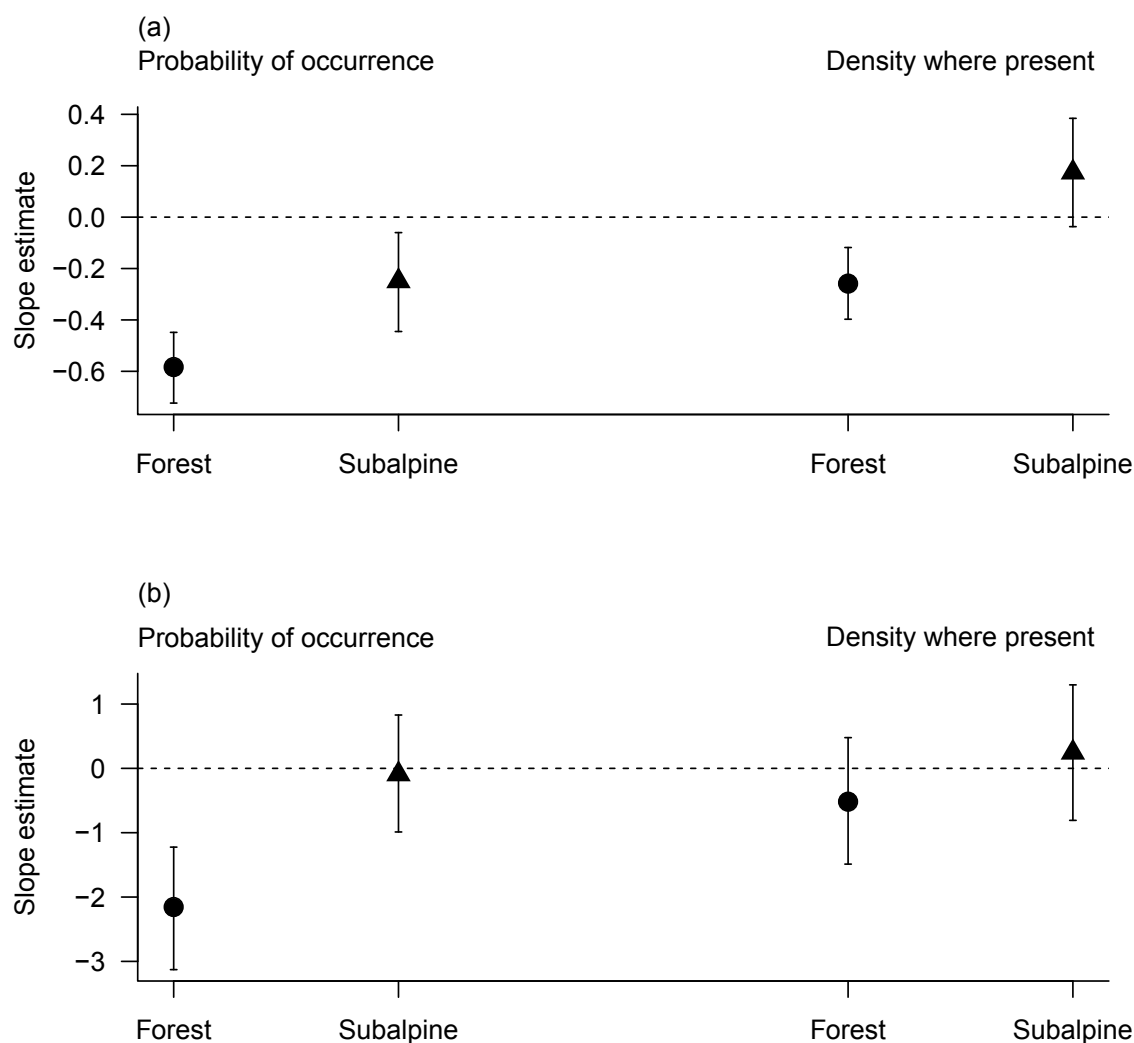


Figure 4. Slope parameter estimates for the relationship between distance of a plot from the creek (log-transformed) and both the probability of *Hieracium lepidulum* presence in a plot, and the density of *H. lepidulum* if present, for plots in forest (circles) and subalpine (triangles) habitats in Craigieburn Forest Park. (a) Slope parameters from a model in which the covariates density of *H. lepidulum* in the creek; elevation; distance up the creek; disturbance and canopy cover (for forest habitat only) were excluded. (b) Slope parameters from a model with these covariates included. Error bars are 95% credible intervals (i.e. the interval within which we are 95% sure the true mean value lies).

If a creek margin source population is present, areas in adjacent habitat that have been locally disturbed by events such as windthrow, landslides and frost-heave in both forest and subalpine habitats are more likely to support populations of *H. lepidulum* than undisturbed areas. Disturbance increases the availability of resources, including soil nutrients and light, reduces competition with resident biota, and is widely recognised in facilitating invasion (e.g. Higgins & Richardson 1998; Hobbs 1991; Lake & Leishman 2004). New Zealand beech forests are extremely species poor, have low light reaching the forest floor, and low soil fertility (Wiser & Allen 2006). *H. lepidulum* invasion in these forests has been positively correlated with soil fertility (Wiser et al. 1998) and light availability (Miller et al. 2014), suggesting that the increase in these resources accompanying disturbance facilitates *H. lepidulum* invasion. Projecting abundances 50 years into the future in the same forest system, Spence et al. (2011) showed that while *H. lepidulum* establishment and abundance were facilitated by minor disturbances, future

abundance in forests was determined more by the persistence of established populations and by propagule pressure from source populations, such as creek margins, than by increases in the frequency of disturbance.

In subalpine habitats, disturbances such as landslides and frost-heave are important in determining the presence of *H. lepidulum*, but not its abundance. This likely reflects an early stage of invasion with smaller source populations and lower rates of propagule supply in these habitats (Fig. 2). Subalpine tussock grassland, scrub and creek-margin habitats have been shown experimentally to be highly susceptible to invasion by *H. lepidulum* in the study area (Miller et al. 2014).

Forest and subalpine habitats display different dynamics in the spread of *H. lepidulum* from source populations. The overall density of *H. lepidulum* is lower in subalpine habitats than in the forest and, as expected given a lack of dispersal barriers in the subalpine habitat, the decline in density with distance from the creek is less pronounced. Additionally, in the subalpine habitat there was no effect of distance from the

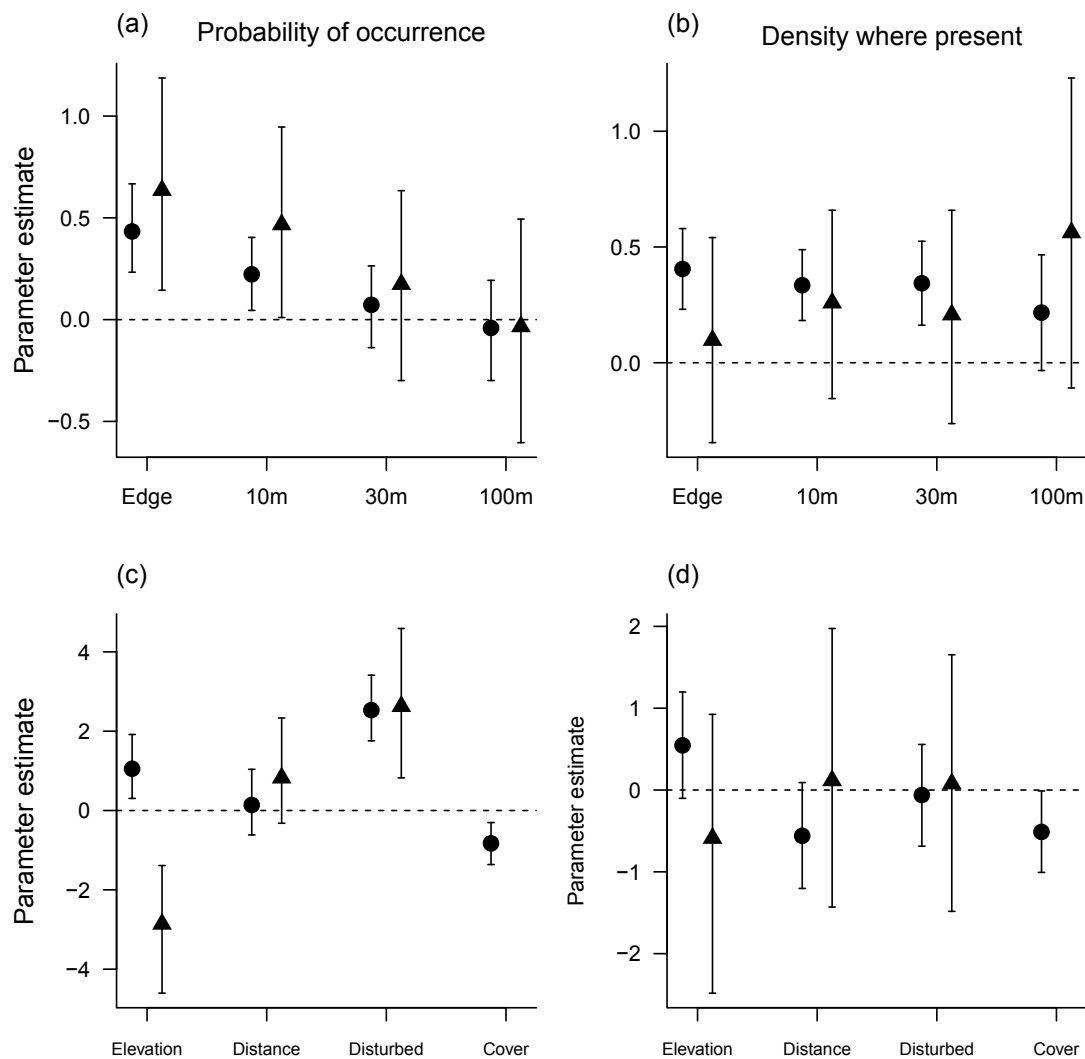


Figure 5. (a, b) Slope parameter estimates for the relationship between local *Hieracium lepidulum* density in the creek margin and both the probability of *H. lepidulum* presence in a plot and the density of *H. lepidulum* where present, for Craigieburn Forest Park plots at different distances away from the creek in forest (circles) and subalpine (triangles) habitats. (c, d) Parameter estimates for relationships between the covariates elevation, distance of transect up creek, disturbance and canopy cover (for forest plots only) and both the probability of *H. lepidulum* presence in a plot and the density of *H. lepidulum* where present, for plots in forest (circles) and subalpine (triangles) habitat. Error bars are 95% credible intervals (i.e. the interval within which we are 95% sure the true mean value lies).

creek on local abundance. Together these results suggest that *H. lepidulum* invasion is at an earlier stage in subalpine areas, that there are few barriers to invasion across this habitat, and that subalpine habitats will become more heavily invaded than forests. Since subalpine habitats are highly susceptible to invasion by *H. lepidulum* (Miller et al. 2014), future spread of this invader in these diverse, biologically important New Zealand plant communities is of conservation concern (but see Meffin et al. 2010).

Management implications

An understanding of the function of source habitats in controlling the spread of invasive species across a complex landscape is essential for managing biological invasions. Indeed, assumptions about habitat invasibility and spread dynamics from source habitats such as roads and riparian habitats often underpin invasive species monitoring programmes, and provide the rationale for setting management

priorities (Maxwell et al. 2009), although these assumptions are often not evidence-based (Byers et al. 2002).

Managers could use our data to design a monitoring programme for *H. lepidulum* in eastern New Zealand mountains, confident that *H. lepidulum* density in forest-creek-margin habitats is a reliable indicator of the extent of *H. lepidulum* invasion into adjacent forest. This is important for prioritising treatment in areas that are still relatively pristine. Rapid, early detection surveys could focus on riparian habitats, and more intensive surveys and treatment could target areas of disturbance such as treefall gaps. Creek networks, roads and tracks in subalpine areas should be targeted (see also Jesson et al. 2000).

Management implications arise from the finding that propagule pressure from populations in source habitats such as creek margins and other disturbed areas are drivers of catchment-wide *H. lepidulum* invasion. First, our results suggest that local propagule pressure is a key determinant of invasion

patterns. Minimising population growth in source habitats will thus likely have a major impact in reducing catchment-wide distribution and abundance. Second, disturbances are a natural part of these ecosystems in both forest and subalpine habitats. Nevertheless, managers should consider the cumulative effects of additional disturbance (such as track, road and building construction) on promoting *H. lepidulum* invasion. This is especially true in subalpine areas where barriers to dispersal and invasion are low.

Acknowledgements

We thank the Miss E.L. Hellaby Indigenous Grasslands Research Trust for funding ALM, Core funding for Crown Research Institutes from the Ministry of Business, Innovation and Employment's Science Innovation Group (SKW), the Department of Conservation and Glenthorne Station for access, and we are grateful to James Scott and Marcus Bridge for field assistance.

References

- Brothers TS, Spingarn A 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* 6: 91–100.
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16: 630–640.
- Cadenasso ML, Pickett STA 2001. Effects of edge structure on flux of species into forest interiors. *Conservation Biology* 15: 91–97.
- Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J 2008a. Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89: 1541–1553.
- Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM 2008b. Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology* 45: 448–458.
- D'Antonio C, Levine J, Thomsen M 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *Journal of Mediterranean Ecology* 2: 233–245.
- DeFerrari CM, Naiman RJ 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *Journal of Vegetation Science* 5: 247–258.
- Dias PC 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* 11: 326–330.
- Duncan RP, Colhoun KM, Foran BD 1997. The distribution and abundance of *Hieracium* species (hawkweeds) in the dry grasslands of Canterbury and Otago. *New Zealand Journal of Ecology* 21: 51–62.
- Elton CS 1958. The ecology of invasions by animals and plants. London, Methuen. 196 p.
- Fletcher D, MacKenzie D, Villouta E 2005. Modelling skewed data with many zeros: A simple approach to combining ordinary and logistic regression. *Environmental and Ecological Statistics* 12: 45–54.
- Flory SL, Clay K 2006. Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. *Plant Ecology* 184: 131–141.
- Forcella F, Harvey SJ 1983. Relative abundance in an alien weed flora. *Oecologia* 59: 292–295.
- Gelbard JL, Belnap J 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17: 420–432.
- Gelman A 2006. Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Analysis* 1: 515–534.
- Gelman A, Hill J 2006. Data analysis using regression and multilevel/hierarchical models. Analytical Methods for Social Research series. Cambridge University Press. 625 p.
- Hansen MJ, Clevenger AP 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological Conservation* 125: 249–259.
- Harris CM, Stanford HL, Edwards C, Travis JMJ, Park KJ 2011. Integrating demographic data and a mechanistic dispersal model to predict invasion spread of *Rhododendron ponticum* in different habitats. *Ecological Informatics* 6: 187–195.
- Harrison S, Hohn C, Ratay S 2002. Distribution of exotic plants along roads in a peninsular nature reserve. *Biological Invasions* 4: 425–430.
- Hewitt AE 2010. New Zealand Soil Classification. Landcare Research Science Series, No. 1, 3rd edition. Manaaki Whenua press. 136 p.
- Higgins SI, Richardson DM 1998. Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. *Plant Ecology* 135: 79–93.
- Hobbs RJ 1991. Disturbance a precursor to weed invasion in native vegetation. *Plant Protection Quarterly* 6: 99–104.
- Jesson L, Kelly D, Sparrow A 2000. The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand. *New Zealand Journal of Botany* 38: 451–468.
- Lake JC, Leishman MR 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* 117: 215–226.
- Maxwell BD, Lehnhoff E, Rew LJ 2009. The rationale for monitoring invasive plant populations as a crucial step for management. *Invasive Plant Science and Management* 2: 1–9.
- McCracken IJ 1980. Mountain climate in the Craigieburn Range, New Zealand. In: Benecke U, Davis MR eds Mountain environments and subalpine tree growth. New Zealand Forest Service Technical Paper 70. Pp. 41–59.
- Meekins JF, McCarthy BC 2002. Effect of population density on the demography of an invasive plant (*Alliaria petiolata*, Brassicaceae) population in a Southeastern Ohio Forest. *American Midland Naturalist* 147: 256–278.
- Meffin R, Miller AL, Hulme PE, Duncan RP 2010. Experimental introduction of the alien weed *Hieracium lepidulum* reveals no significant impact on montane plant communities in New Zealand. *Diversity and Distributions* 16: 804–815.
- Miller AL 2006. Untangling spatial distribution patterns of the invasive herb *Hieracium lepidulum* Stenstr. (Asteraceae) in a New Zealand mountain landscape. PhD thesis, Lincoln University, Canterbury, New Zealand. 146 p.
- Miller AL, Diez JM, Sullivan JJ, Wangen SR, Wiser SK, Meffin R, Duncan RP 2014. Quantifying invasion resistance: the use of recruitment functions to control for propagule pressure. *Ecology* 95: 920–929.

- Naiman RJ, Décamps H 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28: 621–658.
- R Development Core Team 2008. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Rejmánek M 1989. Invasibility of plant communities. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M eds *Biological invasions: a global perspective*. Chichester, John Wiley. Pp. 369–388.
- Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M 2000. Plant invasions – the role of mutualisms. *Biological Reviews of the Cambridge Philosophical Society* 75: 65–93.
- Rose AB, Platt KH, Frampton CM 1995. Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology* 19: 163–174.
- Rose AB, Basher LR, Wiser SK, Platt KH, Lynn IH 1998. Factors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. *New Zealand Journal of Ecology* 22: 121–140.
- Spence LA, Ross JV, Wiser SK, Allen RB, Coomes DA 2011. Disturbance affects short-term facilitation, but not long-term saturation, of exotic plant invasion in New Zealand forest. *Proceedings of the Royal Society B-Biological Sciences* 278: 1457–1466.
- Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M, Son Y 1999. Exotic plant species invade hotspots of native biodiversity. *Ecological Monographs* 69: 25–46.
- Sullivan JJ, Williams PA, Timmins SM, Smale MC 2009. Distribution and spread of environmental weeds along New Zealand roadsides. *New Zealand Journal of Ecology* 33: 190–204.
- Thomas A, O'Hara RB, Ligges U, Sturtz S 2006. Making BUGS open. *R News* 6: 12–17.
- Von Holle B, Simberloff D 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86: 3212–3218.
- Watkins RZ, Chen J, Pickens J, Broszofsky KD 2003. Edge effects of forest roads on understory plants in a managed hardwood landscape. *Conservation Biology* 17: 411–419.
- Wiser S, Allen R 2000. *Hieracium lepidulum* invasion of indigenous ecosystems. *Conservation Advisory Science Notes* 278. Wellington, Department of Conservation. 9 p.
- Wiser SK, Allen RB 2006. What controls invasion of forest understories by alien plants? In: Allen RB, Lee WG eds *Biological invasions in New Zealand*. Ecological Studies 186. Heidelberg and Berlin, Springer. Pp. 195–207.
- Wiser SK, Allen RB, Clinton PW, Platt KH 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79: 2071–2081.
- With KA 2002. The landscape ecology of invasive spread. *Conservation Biology* 16: 1192–1203.

Editorial Board member: Matt McGlone

Received 16 September 2013; accepted 1 April 2014